COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, IV

THE FUSIFORM INITIALS OF THE CAMBIUM AND THE FORM AND STRUCTURE OF THEIR DERIVATIVES

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It has been demonstrated that in both dicotyledons and monocotyledons vessels originated by modification of long tracheids having scalariform pitting (Bailey & Tupper, 1918; Cheadle, 1942, 1943). In the case of the dicotyledons, highly advanced stages in the phylogenetic specialization of vessels occur in plants having short vessel members with simple perforation plates throughout both the primary and secondary xylem (Bailey, 1944). In such plants scalariform perforation plates are eliminated. During the evolutionary specialization of vessels there commonly tend to be concomitant changes in the ground mass of imperforate tracheary cells which, by elimination of the borders of their pits, become libriform fibers, which, in turn, may at times retain their living contents, become septate, and function in the storage of starch (Bailey, 1936).

In dicotyledons, the differentiation of sieve tubes in the secondary phloem has appeared to afford a phylogenetic parallel to the development of vessels in the secondary xylem (Esau, 1953, p. 275; Esau, Cheadle & Gifford, 1953). In both tissues, axial translocation seems to be facilitated by modification in the more or less extensively overlapping ends of adjacent cells in axial seriations: in the xylem by loss of pit membranes to form perforations and in the phloem by formation of sieve plates having larger connecting strands than those in the sieve areas of the lateral walls. Some investigators have suggested that there is a direct correlation between the degree of evolutionary spcialization of sieve plates in the end walls and decrease in conspicuousness of the sieve areas in the lateral walls (Cheadle & Whitford, 1941; Cheadle, 1948; Cheadle & Uhl, 1948; Esau & Cheadle, 1959). Zahur (1959), however, did not find such a correlation.

It should be strongly emphasized in this connection that huge volumes of anatomical data regarding the secondary xylem of dicotyledonous families have accumulated during the last half-century. Wood, in general, is adequately preserved by simple drying, and industrial pressures have stimulated the assembling and study of large collections of wood samples by institutions in various parts of the world. No comparable information is available at present regarding the secondary phloem of dicotyledons.

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Further, as explained by Cheadle (1956), this tissue is difficult to study because of its physiological and structural peculiarities. Even the most extensive reconnaissance to date (Zahur, 1959) deals with only a relatively few representatives of the 85 families sampled.

Furthermore, as one of us (Bailey, 1957) has emphasized: "There are certain details of the trends of specialization in the xylem which need to be more clearly and generally understood in shifting from a consideration of the dicotyledons *as-a-whole* to investigations of the taxonomy of individual taxa of restricted size. In revealing salient trends of evolutionary specialization by analyses of data obtained from the dicotyledons *as-a-whole*, variations due to obtaining specimens from different parts of the plant, from plants of different growth rates, from genetically different taxa, etc., tend to neutralize one another. In addition, various localized, divergent trends of specialization do not obscure or confuse the major trends of evolution in the dicotyledons *as-a-whole*. However, when one becomes concerned with taxa of decreasing size, viz. families, subfamilies, tribes, genera and species, such variations and deviations become increasingly significant."

For example, data from the dicotyledons as-a-whole clearly reveal evolutionary changes from scalariform to simple perforation plates, and from scalariform to alternate multiseriate intervascular pitting. In any randomly selected minor taxon, one of these trends may be retarded or accelerated in relation to the other. Therefore, with present inadequate information regarding the secondary phloem in most orders, families, and genera, it is not possible to determine with certainty what some of the more important trends of phylogenetic specialization in the dicotyledons as-a-whole may actually be. This is particularly the case in those parenchymatous cells that are physiologically and ontogenetically related to sieve elements.

During the phylogenetic specialization in the secondary tissue of dicotyledons, there is a progressive shortening of fusiform cambial initials which not infrequently culminates in storied forms of cambia, involving longitudinal rather than pseudotransverse anticlinal divisions and the elimination of intrusive elongation following such divisions (Bailey, 1923).

In general, the phylogenetic shortening of fusiform cambial initials is most closely paralleled in the secondary xylem and phloem by shortening of fusiform parenchymatous derivatives and by changes in the length of parenchyma strands (for *ordinarily* fusiform parenchymatous cells and the mother cells of parenchyma strands do not elongate during tissue differentiation). As a concomitant of shortening fusiform cambial initials, the parenchyma strands commonly tend to be composed of fewer and generally of shorter cells.

Statistical data obtained from the dicotyledons as-a-whole indicate that shortening of the fusiform initials likewise is closely reflected in the length of vessel members, there being only slight elongation at times during the maturation of primitive, long, slender vessel members, and a slight contraction at times during the differentiation of short, very broad, highly

specialized ones. On the contrary, fiber-tracheids and libriform fibers become longer than the fusiform cambial initials from which they are derived owing to more or less extensive intrusive elongation during tissue differentiation.

In the secondary phloem of such vesselless gymnosperms as the Pinaceae, Taxodiaceae, and Cupressaceae, statistical averages indicate that sieve cells simulate fusiform cambial initials in length, there being no appreciable elongation, as occurs at times in tracheids, during their maturation from cambial initials. In the phylogenetically specialized dicotyledons having very short fusiform cambial initials, particularly those having storied cambia, the sieve-tube members in statistical averages closely simulate the fusiform initials in length. On the contrary, in some dicotyledons having less highly specialized cambia, the parallelism in length may be modified by more or less numerous divisions of mother cells prior to the formation of sieve-tube members, companion cells, and some parenchymatous cells (cf. Esau & Cheadle, 1955; Cheadle & Esau, 1958; Zahur, 1959). In such plants, the sieve-tube members tend statistically to be considerably shorter than fusiform cambial initials.

Statements in the literature regarding detailed structure of the xylem and phloem of leaf-bearing cacti are casual and fragmentary and are based largely upon *Pereskia aculeata* Mill. The occurrence of septate libriform fibers and porous vessels in the wood of this species is recorded by Schenck (1893) and Solereder (1899). If the most primitive living cacti occur among the leaf-bearing ones, as is generally assumed to be the case, it is essential to obtain comprehensive information regarding the levels of phylogenetic specialization that they have attained, particularly for future use in understanding trends of increasing structural specialization that occur in the Opuntieae and Cereeae.

In all of the putative species of *Pereskia*, *Pereskiopsis*, and *Quiabentia* that we have studied (mentioned in previous papers of this series [Bailey, 1960, 1961a, 1961b]) the fusiform initials of the cambium have attained a high level of evolutionary modification. They are comparatively short, commonly ranging in length from only 150 to 400 microns. Although they are not consistently in perfect storied or stratified arrangement, they frequently exhibit a tendency to become storied, at least in some parts of a mature plant. Where they approach a perfect storied arrangement, they have abruptly tapered ends and a hexagonal form as seen in tangential longitudinal sections of the cambium (FIG. 1) and the cells of one stratum do not extensively overlap those of higher and lower levels. On the contrary, where stratification is imperfect, the cells have more gradually tapered ends, and there is more overlapping of the cells of different levels (FIG. 4). It should be noted in this connection that where stratification occurs in the leaf-bearing cacti it tends to differ from that which occurs in plants of other dicotyledonous families in exhibiting a conspicuous tendency for the strata of fusiform initials to have a diagonal, rather than a transverse, orientation as seen in tangential longitudinal sections of the cambium.

In dicotyledons having very short, especially storied, cambial initials, where adequately preserved material of the cambium is not available, the length and the arrangement of fusiform initials may be detected both in certain of their derivatives in the xylem and in recently formed phloem.

The distribution of wood parenchyma in *Pereskia*, *Pereskiopsis*, and *Quiabentia* is of a specialized paratracheal rather than a primitive apotracheal form, but more or less extensive arcs of thick-walled lignified or thin-walled unlignified parenchyma occur at times and may prove to be associated in some manner with successive zones of growth in the enlargement of stems and roots. The fusiform parenchymatous cells and parenchyma strands are short, the latter being composed usually of two or three cells only. In tangential longitudinal sections of the secondary xylem, the fusiform parenchyma and parenchyma strands (where not deformed and displaced by excessive enlargement of vessels) closely simulate fusiform cambial initials in overall form. Furthermore, where parenchyma is sufficiently abundant, particularly in areas of zonal distribution, the arrangement of fusiform cambial initials, whether storied or nonstoried, is clearly revealed by the arrangement of the parenchymatous cells.

The vessels in stems and roots of the leaf-bearing cacti are of a highly advanced evolutionary form having simple perforation plates throughout the primary (FIG. 8) and secondary xylem (FIG. 5). In the secondary xylem, the vessels vary markedly in diameter from 20 microns to as much as 200 microns in certain cases. The vessels occur independently and in clusters of varying size and form. The smaller vessels, as seen in transverse sections, are angular, whereas the larger ones are more nearly circular or oval, except where they are modified by compression in clusters. Such variations in the vessels occur, not only in different species and different parts of a single plant, but also in closely adjacent areas of the secondary xylem. The members of the smallest vessels (i.e., those which do not expand appreciably in tangential diameter during maturation) resemble fusiform cambial initials in overall form when viewed in tangential longitudinal sections of the xylem. In such sections, the vessel members may be confused with vascular tracheids, but the perforations in their more or less abruptly tapered ends are clearly visible in radial longitudinal sections. Where sufficiently abundant, and particularly in association with parenchyma, such small vessel members reveal a storied (FIG. 2) or nonstoried arrangement of fusiform initials in the cambium.

In the secondary xylem of the leaf-bearing cacti, vessel members of the smallest diameter tend to have diagonally oriented perforation plates in their terminal radial walls. Larger vessel members, although as short or shorter than fusiform cambial initials, vary more or less markedly in form owing to excessive lateral enlargement during their maturation. The perforation plates, consisting of a circular or oval opening surrounded by a clear zone of unpitted wall, may be transversely (FIG. 5) or more or less diagonally oriented. Furthermore, where vessels are closely associated

in larger clusters and where vessels deviate from a longitudinal course to pass diagonally through the broad multiseriate rays (FIGS. 6, 7), the vessel members may at times have perforation plates in their sides rather than in their more or less inclined ends.

The bordered pitting in the sides of adjoining vessels tends to be of the evolutionarily advanced alternate-multiseriate form (FIGS. 9, 11), but areas of scalariform pitting (FIGS. 12, 13) and of opposite-multiseriate pitting are of not infrequent occurrence. The bordered pits of multiseriate arrangements vary in size and considerably in form from circular to oval and to angular where the pits are closely crowded. (Compare FIGS. 9, 11, 13, 15, 16.) The pit apertures likewise vary from small, nearly circular (FIG. 9), to oval (FIG. 15), and to transversely slitlike (FIG. 13). Furthermore, the borders of the pits exhibit at times reduction in conspicuousness in relation to the size of the apertures. (Compare FIGS. 11, 15, 16.) In areas of scalariform pitting, unconformity in the pitting of the walls of adjacent vessels frequently occurs (FIGS. 12, 13), i.e., a transversely extensive pit in one wall being related to smaller pits in the adjoining vessel wall.

The pits of vessels in contact with wood parenchyma and rays exhibit a wide range of variability. At times, they closely resemble those of intervessel contacts in size, form, and arrangement. (Compare FIGS. 9, 10; 13, 14; 16, 18.) However, in the case of the leaf-bearing cacti, there commonly is a conspicuous tendency for vessel pits in contact with parenchyma to have enlarged apertures and to reduce or eliminate their bordering area (FIG. 20). In other words, the pits in the walls of vessels in contact with parenchyma become simple pits in conformity with the unbordered pits of adjacent parenchymatous cells. Where vessels are completely jacketed by wood parenchyma and have large, transversely elongated unbordered pits, the vessel members, when isolated by maceration, resemble vessel members of those parts of the primary xylem which have reticulate forms of wall thickening (FIG. 22).

The libriform fibers of the leaf-bearing cacti, unlike the vessel members, fusiform wood parenchyma, and parenchyma strands, elongate more or less extensively by intrusive elongation during tissue differentiation. Therefore, they (FIGS. 24–27) become longer than the fusiform cambial initials (FIG. 23) from which they are derived. However, the amount of elongation varies greatly, not only in different parts of a plant, but also in closely adjacent parts of the secondary xylem. In some cases, the elongation at one or both ends of the cell is only a few microns, whereas, in other cases, the elongation at both ends of the cell is extensive. Thus, libriform fibers may be only slightly longer than the fusiform cambial initials from which they are derived, i.e., 150–400 microns (FIG. 24) or they may attain maximum lengths of as much as 1000–1300 microns (FIGS. 26, 27). Some libriform fibers are relatively slender and taper gradually and uniformly toward their ends (FIG. 26); others are broader in their central part and taper abruptly at one or both ends into long narrow tips (FIGS. 25, 27). In both instances the small oval or slitlike simple pits tend to be concentrated in the central part of the fibers which corresponds roughly in length

to that of the fusiform cambial initials. (Compare FIG. 23 with FIGS. 24–27.)

The slitlike pits usually are oriented more or less diagonally to the long axis of the cell but may at times be oriented parallel to its axis. This indicates that the orientation of cellulosic microfibrils in the central or S_2 layer of the secondary wall may, at least occasionally, deviate from helical to longitudinal.

The fibers in any particular part of the secondary xylem may be prevailingly septate (usually a single septum to each cell, FIG. 26), nonseptate, or in varying mixtures of septate and nonseptate. Both the septate and the nonseptate (FIGS. 17, 19, 21) fibers retain their protoplasts and nuclei and are capable, at least in certain parts of the plant or at certain seasons of the year, of storing abundant starch.

In the members of *Pereskia*, *Pereskiopsis*, and *Quiabentia* which we investigated, the phloem derivatives, viz., sieve elements and parenchyma, as seen in tangential longitudinal sections in close proximity to the cambium, commonly reflect the form and distribution of the fusiform cambial initials (FIGS. 3, 4). The fusiform parenchyma and parenchyma strands, however, are more reliable indicators of the overall form of fusiform initials than are the sieve elements. This is because the sieve-tube members commonly differentiate in one or more parts of a cell complex that results after longitudinal and sometimes transverse divisions in a single phloem mother cell. Therefore, although the length of sieve-tube members in statistical averages generally corresponds to that of the fusiform cambial initials, their overall form frequently does not. The phloem-parenchyma strands are usually composed of two or three cells arranged in a vertical file and appear to originate by divisions in a single phloem mother cell.

The sieve-tube members present features of advanced structural specialization. The sieve plates commonly occur in the more or less transverse (FIG. 28) or slightly oblique end walls (FIGS. 29, 30) but sometimes may be present in the lateral walls (FIG. 29). In certain cases, sieve plates may not be present at both ends of a sieve-tube element but may occur only at one end and in one of the lateral walls (FIG. 29). Usually the pores and the callose cylinders are distributed rather evenly throughout the sieve plate and the latter may be interpreted as a simple sieve plate. Occasional variations in sieve-plate structure occur, however. In some sieve elements with somewhat sloping end walls the pores and the callose cylinders may be distributed in two or more distinct groups in the sieve plate (FIGS. 30, 31). There is no strict uniformity with regard to the distribution of these two forms of sieve plates. They occur in different parts of the same plant and even at the two ends of a single sieve-tube member. These variations in sieve-plate structure are related in a general way to the orientation of the end walls in the sieve elements which, in turn, seems to be related to the character and orientation of end walls in the fusiform cambial initials (FIG. 23).

In addition to sieve plates which usually occur at or near their end walls, sieve-tube members have numerous small sieve areas that are scattered

throughout both radial and tangential lateral walls (FIG. 32). The pores and their callose cylinders in these sieve areas are much smaller than those in the sieve plates. (Compare FIGS. 31, 32.) The size of these lateral sieve areas, as determined by the number of callose cylinders stained with lacmoid in one area, varies considerably. In the same sieve-tube member, some lateral sieve areas may be very small, composed of one or two strands and their callose cylinders only, whereas others may be composed of several strands and their callose cylinders.

Generally, one or more companion cells occur in association with a sieve-tube member (FIGS. 28, 29). In addition, one or more members of a cell complex, in which sieve-tube elements and companion cells arise, may differentiate as parenchymatous elements. The exact relationships between the different cells that originate after divisions in a single phloic mother cell and the sieve-area connections between them require detailed ontogenetic study.

During the transition from "functional" to "nonfunctional" phloem [3] the parenchymatous cells of both the axially oriented part and the rays retain their living contents, capacity for division, and commonly undergo more or less extensive changes in size and form. The most striking changes of taxonomic significance are those which occur in the nonfunctional phloem of *Pereskia*, these being absent in *Pereskiopsis* and *Quiabentia*. As one of us has shown (Bailey, 1961a) three distinct categories of pereskias can be segregated upon the basis of differences in the formation of sclereids in the nonfunctional part of the secondary phloem. In two of these categories of species, sclereid formation involves extraordinary enlargements of parenchymatous cells in both diameter and length. In the third category, the changes in size and form are more nearly comparable to those that occur in the formation of ordinary sclereids.

Although crystals are commonly present in the ray parenchyma of functional phloem in all three genera, they rarely, if ever, occur in axially oriented parenchyma. However, they do occur at times in axial parenchyma of nonfunctional phloem (Bailey, 1961b). Variations in the presence and form of these crystals may prove to be of some taxonomic significance when more adequate and extensive collections are available for detailed investigation.

DISCUSSION

It is evident from our reconnaissance of the secondary vascular tissues of *Pereskia*, *Pereskiopsis*, and *Quiabentia* that these tissues have attained highly advanced levels of evolutionary specialization. This is shown, for example, by the dimensions and form of the cambial fusiform initials and their derivatives, by the perforation plates and the lateral pitting in vessels, by the storage of starch in both septate and nonseptate libriform fibers, and by the distribution patterns of vessels and wood parenchyma.

[3] Following Esau (1953, p. 299) "nonfunctional" phloem refers to that part of the phloem in which sieve elements and companion cells have ceased to function.

Such evidence at least suggests that the early leaf-bearing representatives of the Cactaceae (those of nearly typical dicotyledonous woody arborescent and shrubby form) had attained high levels of internal anatomical specialization before increasing succulence and other morphological changes led to the differentiation of the Opuntieae and Cereeae.

The ranges of anatomical variability in different parts of a single plant and in the same clone when grown under different environmental influences are very extensive. Potential diagnostic criteria, such as differences in the size, form, and distribution of the constituent cells of xylem, in the form and orientation of perforation plates; in pitting between vessels and between vessels and parenchyma; in the presence or absence of septa in libriform fibers, etc. (which have been utilized so commonly in the differentiation of taxa in other dicotyledonous families) appear, in general, in the leaf-bearing Cactaceae to be of a quantitative rather than a qualitative character. Likewise, in phloem, the orientation of the sieve plates near the ends of sieve-tube members may vary from more or less oblique to perfectly transverse, and the number of pore groups (viz., sieve areas) on the sieve plate may range from one to three or more. The difference between the size of pores and connecting strands in the lateral sieve areas *versus* the sieve plates is very great in all species of the three leaf-bearing genera. Therefore, in the case of these cacti, large volumes of material must be studied statistically in order to attain results of valid taxonomic significance.

In the past, unjustifiable phylogenetic and taxonomic inferences have resulted from comparisons between the frequency of diagonal and transverse orientations of terminal perforation plates in closely related taxa without taking into consideration various factors involved in the statistical differences. Important influences in this connection are the length of fusiform cambial initials, the amount of transverse enlargement of vessel members during tissue differentiation, the deformation when vessels occur in crowded clusters, and the aberrations produced in xylem of distorted or burly grain. In straight-grained xylem of the leaf-bearing cacti, the broader vessel members tend, on an average, to have transversely or nearly transversely oriented terminal perforation plates, whereas the narrowest vessels commonly have diagonally oriented ones. Where the grain of the xylem is distorted, as so frequently happens in stems and roots of the leaf-bearing cacti (owing in large measure to the frequent diagonal dissection of broad rays by conversion of ray initials to fusiform ones), steeply diagonal and even laterally placed perforation plates are of not infrequent occurrence. Similar aberrations occur in the orientation of sieve plates in the phloem. From the point of view of salient trends of phylogenetic specialization in the dicotyledons *as-a-whole*, the occurrence of simple perforation plates throughout both the primary and secondary xylem is of greater evolutionary significance than are deviations from a transverse orientation of perforation plates in the vessels of certain parts of the stems and roots of the leaf-bearing cacti.

The occurrence of septate libriform fibers in various dicotyledonous

families has been based largely upon surveys made of dried wood samples. It should be recognized, in this connection, that a great many of the samples consist of heart-wood. Where specimens of undecayed sapwood are available, they are sectioned after boiling in water and frequently after softening treatment in hydrofluoric acid. Such sections do not contain starch, but the assumption is made, probably correctly, that the septate fibers in the sapwood retained their living protoplasts at functional maturity and were capable, at least for a time, of storing starch. The common occurrence of starch in nonseptate libriform fibers of the leaf-bearing cacti raises the question whether the storage of starch in nonseptate fibers of sapwood is not of much commoner occurrence in dicotyledons than has been realized. From physiological as well as phylogenetic points of view, the whole problem of retention of living protoplasts and storage of starch in nonseptate libriform fibers, whether confined to newly formed sapwood, whether capable of seasonal depletion and renewal as in the case of starch in ray tissue, etc., needs to be thoroughly investigated, not only in the Cactaceae, but also in other families of the dicotyledons.

In this paper, we have omitted discussion of ray initials in the cambium and of their derivatives in the xylem and phloem. The rays in the leaf-bearing Cactaceae are obviously of a highly specialized form, being prevailingly multiseriate, uniseriate rays having been eliminated. It seems best to discuss rays in subsequent papers of this series, dealing in greater detail with the structure of various putative species of *Pereskia*, *Pereskiopsis* and *Quiabentia*.

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EXPLANATION OF PLATES

PLATE I

FIGS. 1–4. TANGENTIAL LONGITUDINAL SECTIONS OF CAMBIUM, XYLEM AND PHLOEM, × 110. 1, *Pereskia cubensis* Britt. & Rose [Atkins Gard.], storied fusiform initials of the cambium. 2, *Pereskiopsis blakeana* Ortega [*Kimnach & Moran 82*], diagonally storied vessel members and wood-parenchyma strands. 3, *Pereskia autumnalis* (Eichlam) Rose [*Moore 8210*], storied sieve-tube members; terminal sieve plates are black. 4, *Pereskia* aff. *sacharosa* Griseb. [*Cárdenas*], imperfectly storied cambial fusiform initials (left of ray) and phloem derivatives (right of ray).

PLATE II

FIGS. 5–8. OCCURRENCE AND ORIENTATION OF SIMPLE PERFORATION PLATES IN VESSEL MEMBERS. 5, *Pereskia grandifolia* Haw. [*Castellanos*], transverse section of the secondary xylem showing transversely oriented perforation plates, × 260. 6, *Pereskia colombiana* Britt. & Rose [*Romero*], radial longitudinal section of the secondary xylem showing laterally placed perforation plate, × 260. 7, *Pereskia nicoyana* Web. [*Rodríguez 662*], tangential longitudinal section of the secondary xylem showing divergence of vessel members through multiseriate ray; vessel members at right have perforation plates, as seen in sectional view at (X), in their lateral radial walls, × 180. 8, *Pereskiopsis aquosa* (Web.) Britt. & Rose [*Dressler*], radial longitudinal section of the primary xylem showing perforation plates in helically thickened vessel members, × 260.

PLATE III

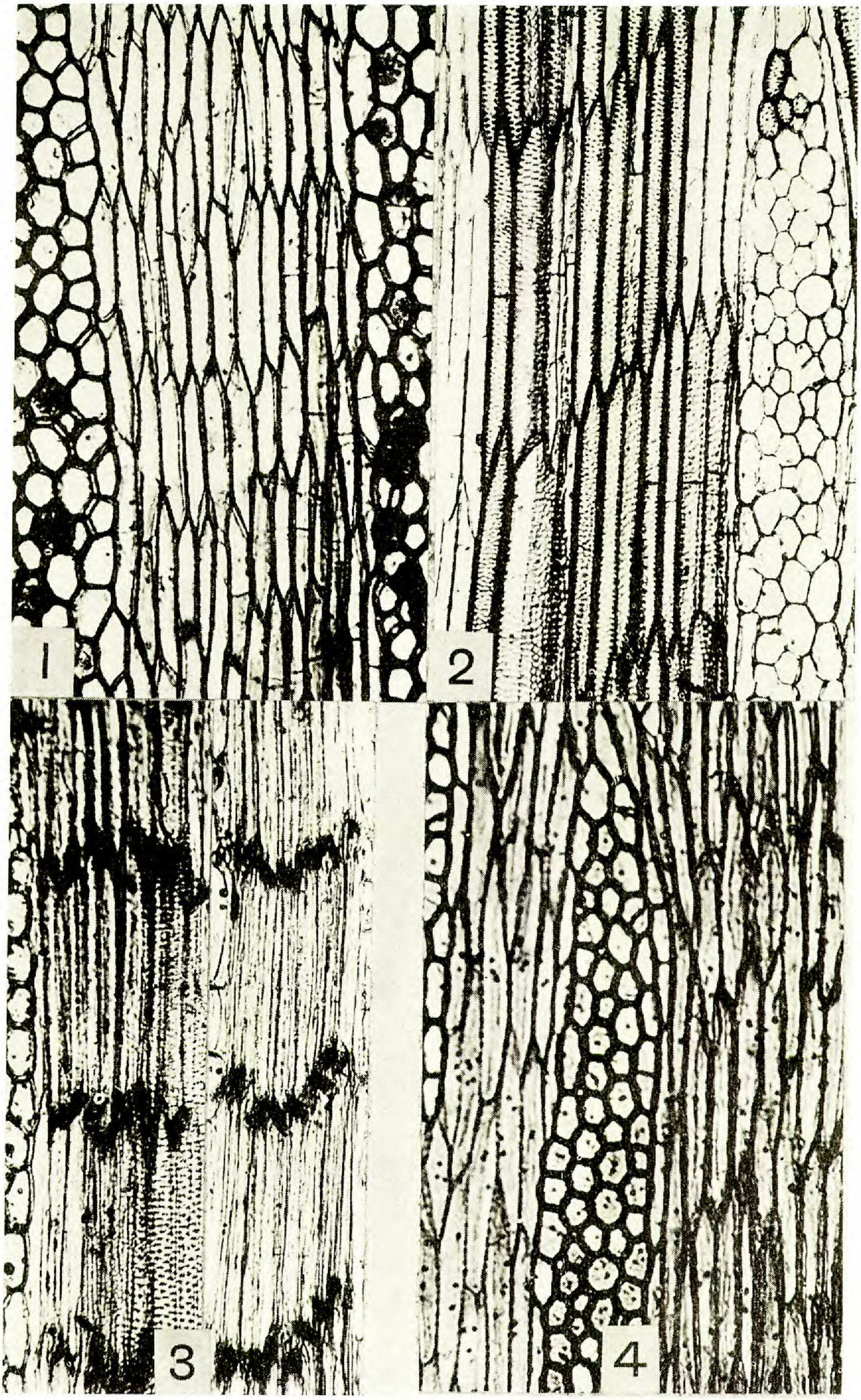
FIGS. 9–15. PITTING BETWEEN VESSELS AND BETWEEN VESSELS AND PARENCHYMA. 9, *Pereskia grandifolia* [*Castellanos*], crowded alternate-multiseriate pitting in walls of contact between vessel members, × 410. 10, *Pereskia colombiana* [*Romero*], pitting between vessel and ray parenchyma, × 410. 11, *Pereskia grandifolia* [*Castellanos*], variations in form of bordered pits and their apertures, × 1130. 12, *Pereskia colombiana* [*Romero*], unconformity in the pitting of vessels; many of the transversely elongated pits in the wall of one vessel are in contact with rows of shorter pits in the wall of the adjoining vessel, × 960. 13, *The same*, scalariform and transitional pitting in lateral walls of adjoining vessels, × 410. 14, *The same*, scalariform pitting between vessel and parenchyma, × 410. 15, *Quiabentia* aff. *chacoensis* Backbg. [Tucumán], bordered pits with large apertures in the lateral walls of adjoining vessels, × 410.

PLATE IV

FIGS. 16–22. LONGITUDINAL SECTIONAL VIEWS OF VESSELS, PARENCHYMA AND NONSEPTATE LIBRIFORM FIBERS. 16, *Pereskiopsis blakeana* [*Kimnach & Moran 82*], reduction in the borders and increase in size of apertures in intervascular pitting, × 410. 17, *Pereskia aculeata* Mill. [Atkins Gard.], iodine stained starch in a nonseptate libriform fiber, × 750. 18, *Pereskia bleo* DC. [Atkins Gard.], reduction in borders and increase in size of apertures in pitting between vessel and ray parenchyma, × 410. 19, *Pereskiopsis chapistle* Britt. & Rose [*Boke B–3*], nuclei (black) and unstained starch in nonseptate libriform fibers, × 1000. 20, *Pereskiopsis blakeana* [*Kimnach & Moran 82*], pitting between vessels and parenchyma, × 410. 21, *Quiabentia* aff. *chacoensis* [Tucumán], nucleus with nucleolus in nonseptate libriform fiber, × 1000. 22, *Quiabentia pereziensis* Backbg. [*Cárdenas*], large unbordered pits between vessel and parenchyma, × 410.

PLATE V

FIGS. 23–32. DIAGRAMMATIC ILLUSTRATIONS OF CAMBIAL FUSIFORM INITIALS, LIBRIFORM FIBERS AND SIEVE-TUBE MEMBERS. 23, *Pereskia sacharosa* [Tucumán], fusiform cambial initials, drawn from tangential longitudinal section of cambium. 24, *Pereskia conzattii* Britt. & Rose [*Dressler*], libriform fiber drawn from maceration. 25, *Pereskia aculeata* [Atkins Gard.], libriform fiber drawn from maceration. 26, 27, *Pereskia conzattii* [*Dressler*], septate and nonseptate libriform fibers drawn from maceration. 28, *Pereskia sacharosa* [Tucumán], sieve-tube member and companion cells, drawn from tangential longitudinal section of phloem. 29, *Pereskiopsis* aff. *chapistle* [*Boke B–3*], sieve-tube member and companion cell, drawn from tangential longitudinal section of phloem. 30, *The same*, sieve-tube member drawn from radial longitudinal section. 31, *The same*, part of a sieve plate, drawn from radial longitudinal section of phloem. 32, *The same*, lateral sieve areas, drawn from radial longitudinal section, companion cell on right. Figures 23–30, × 175; figs. 31, 32, × 875.



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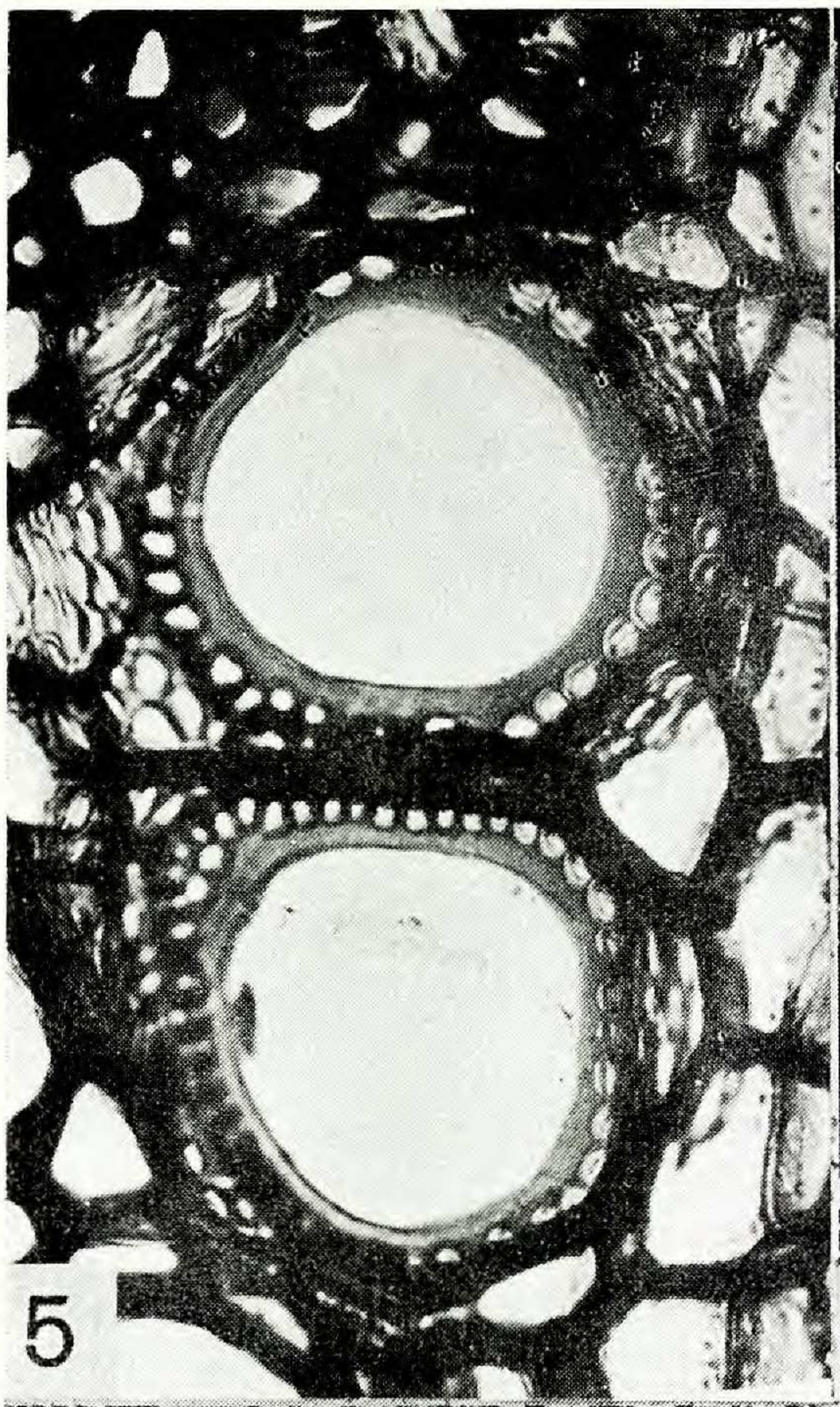

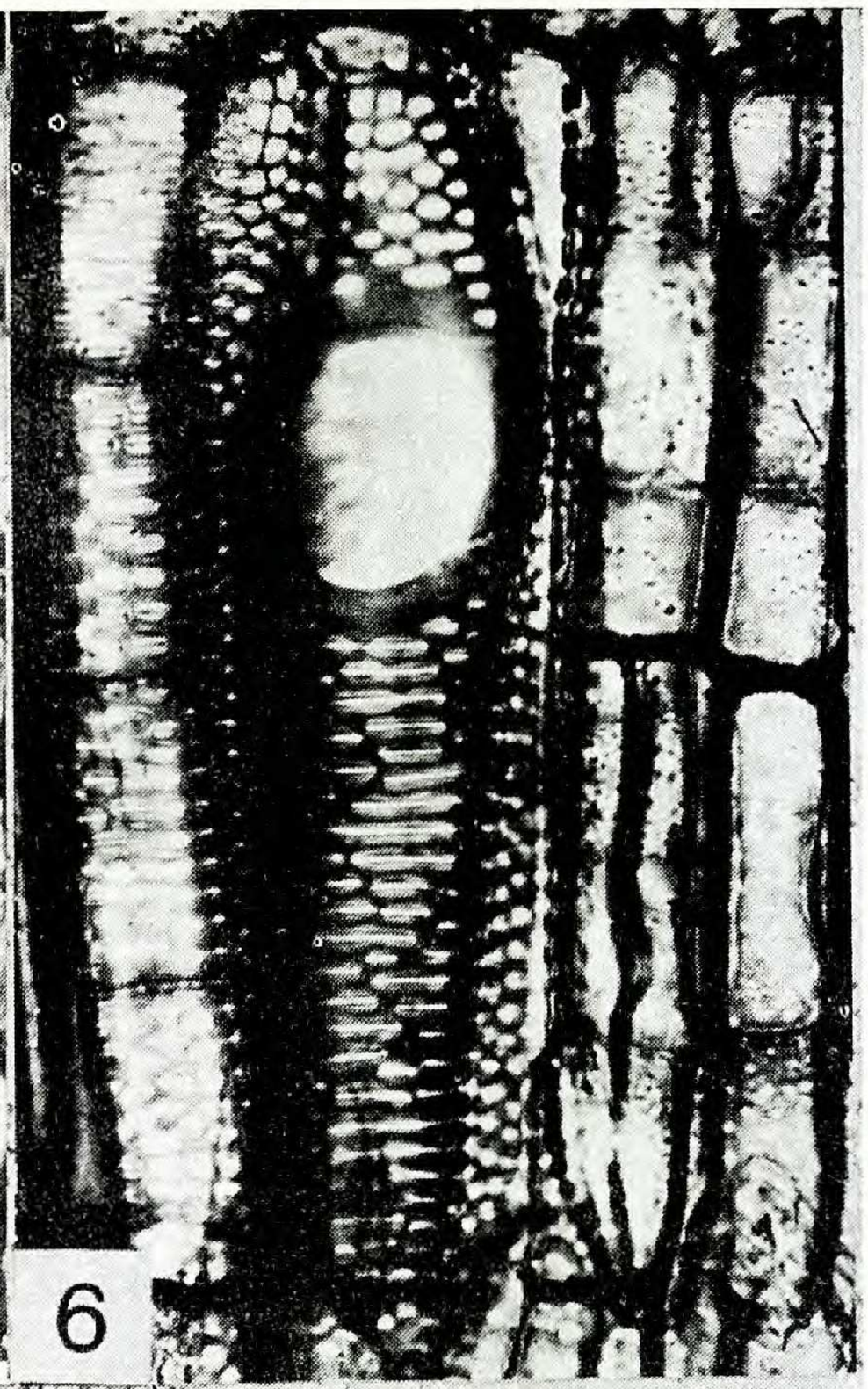

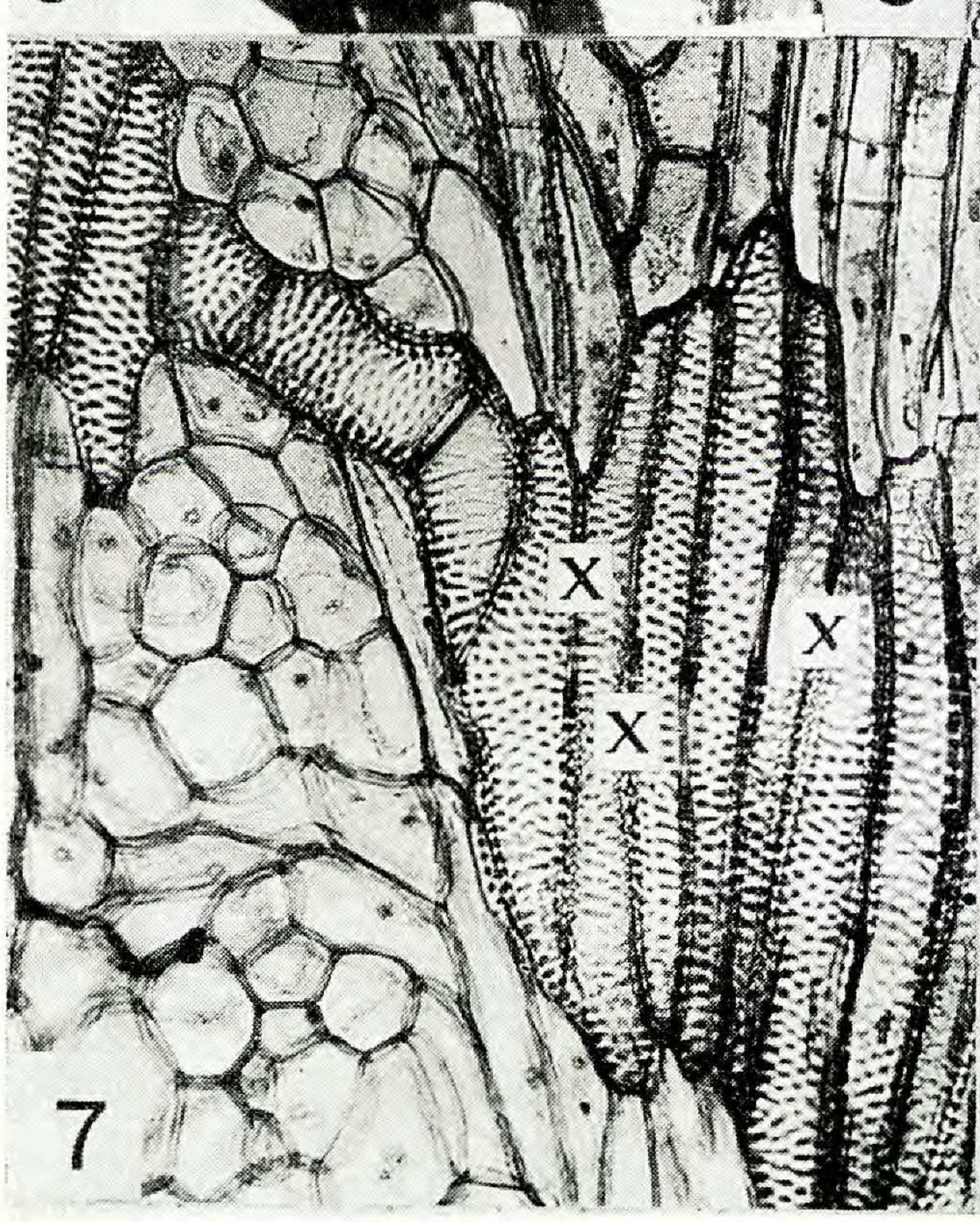

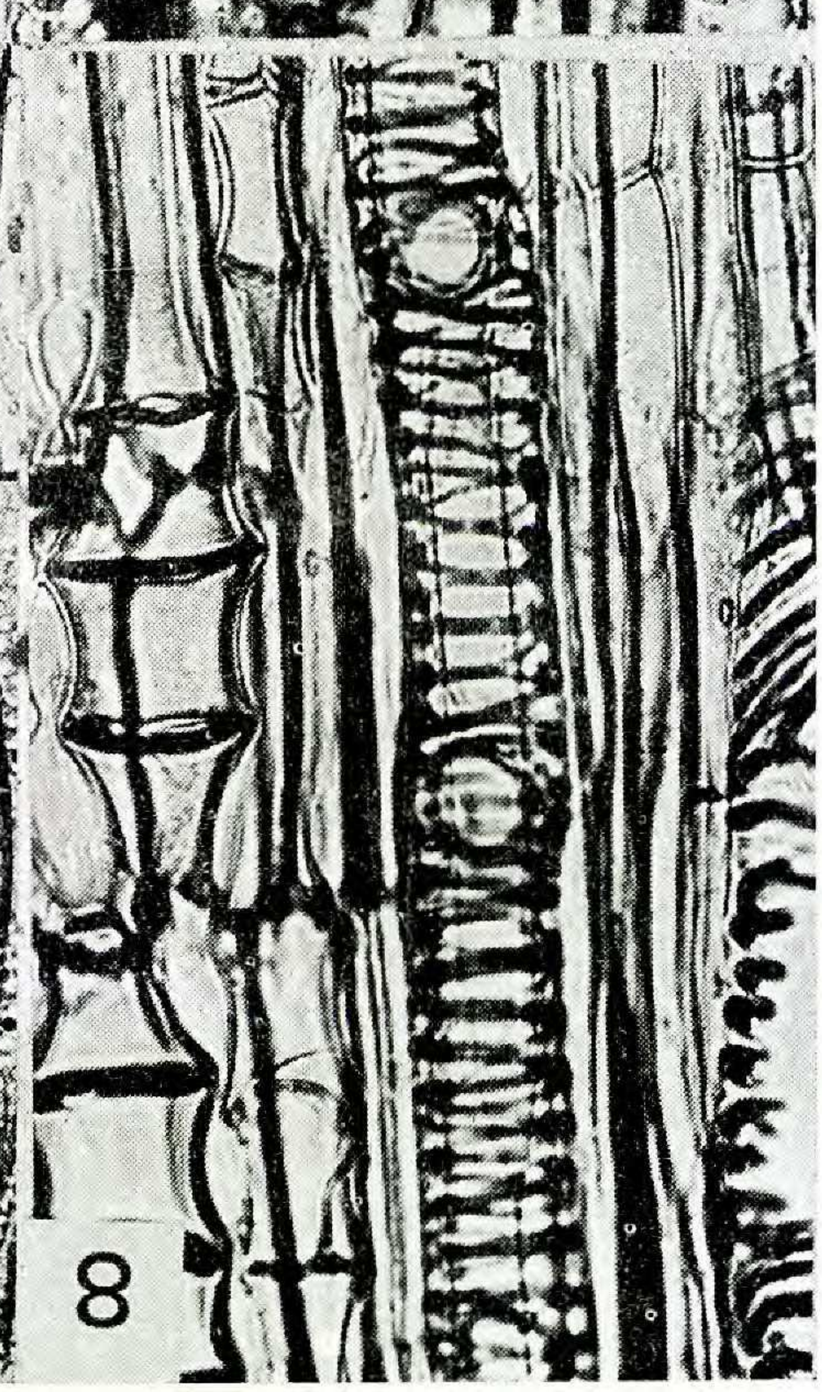

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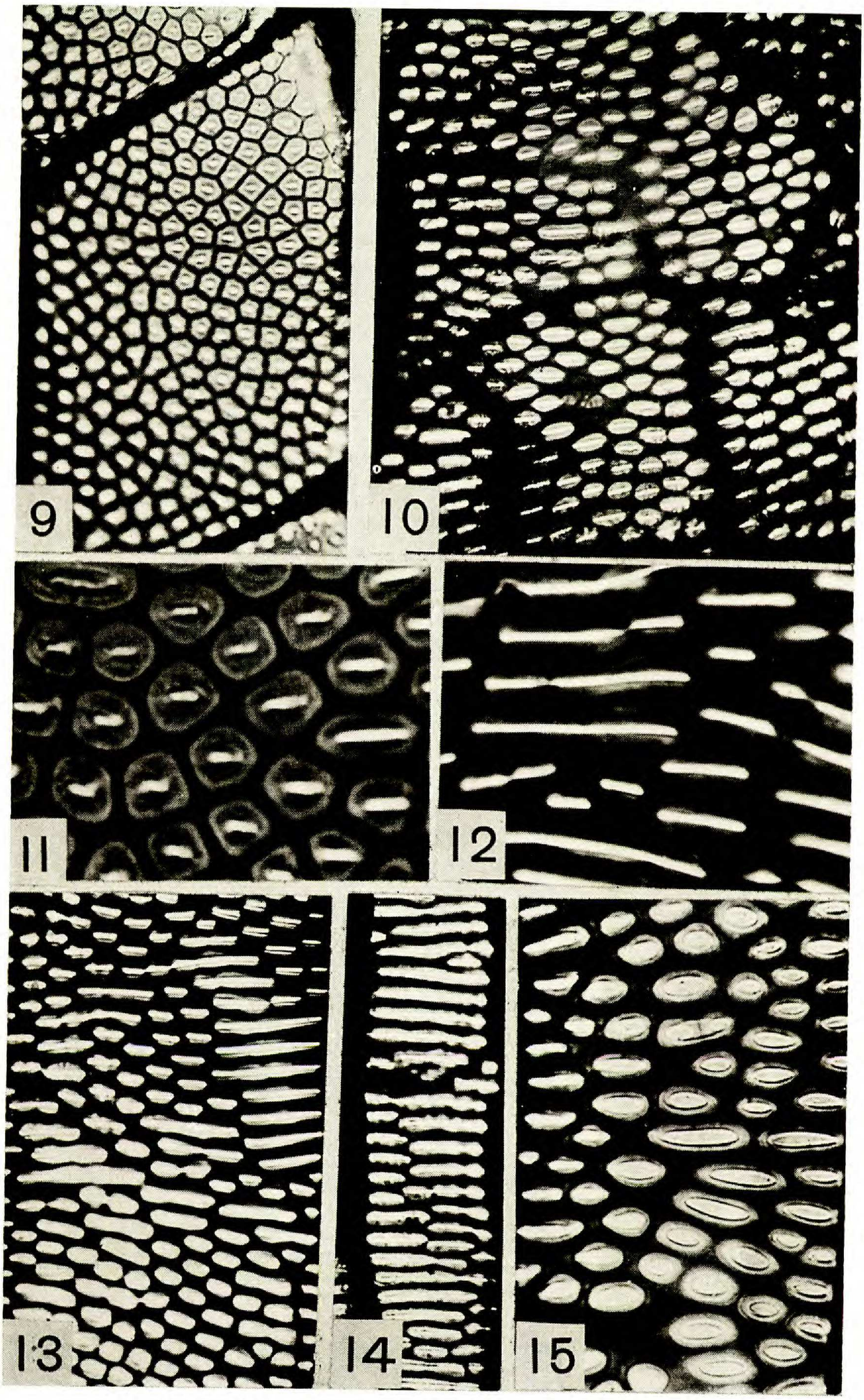

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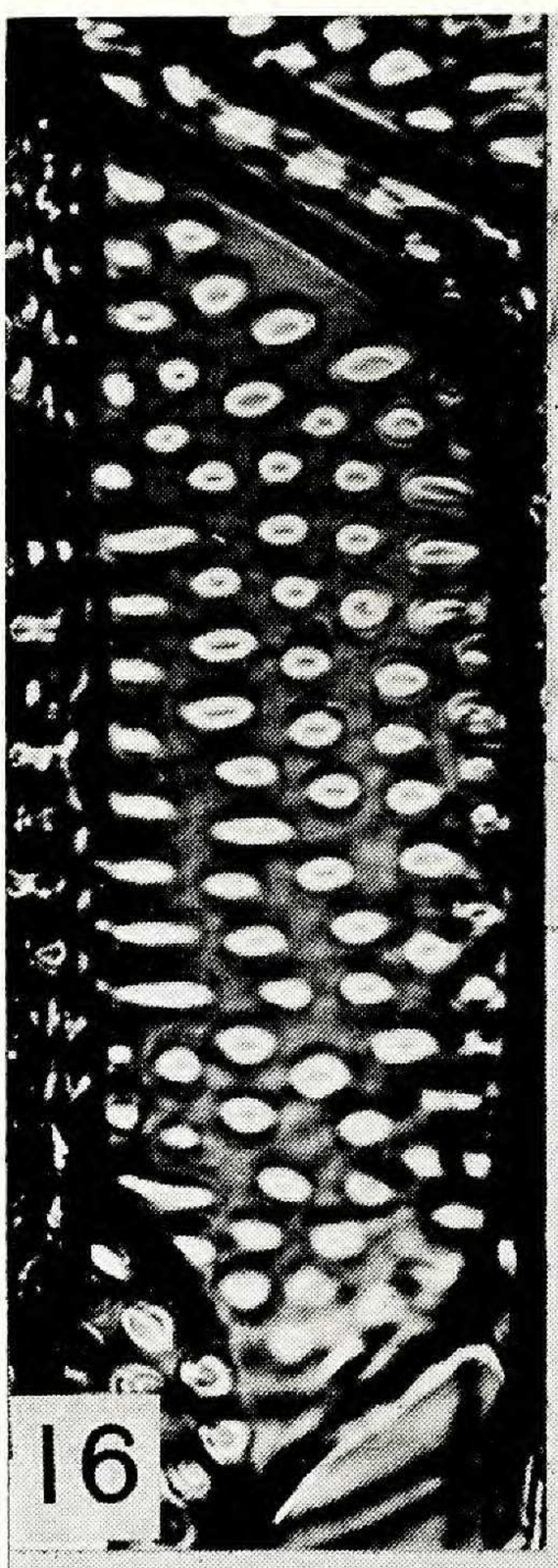
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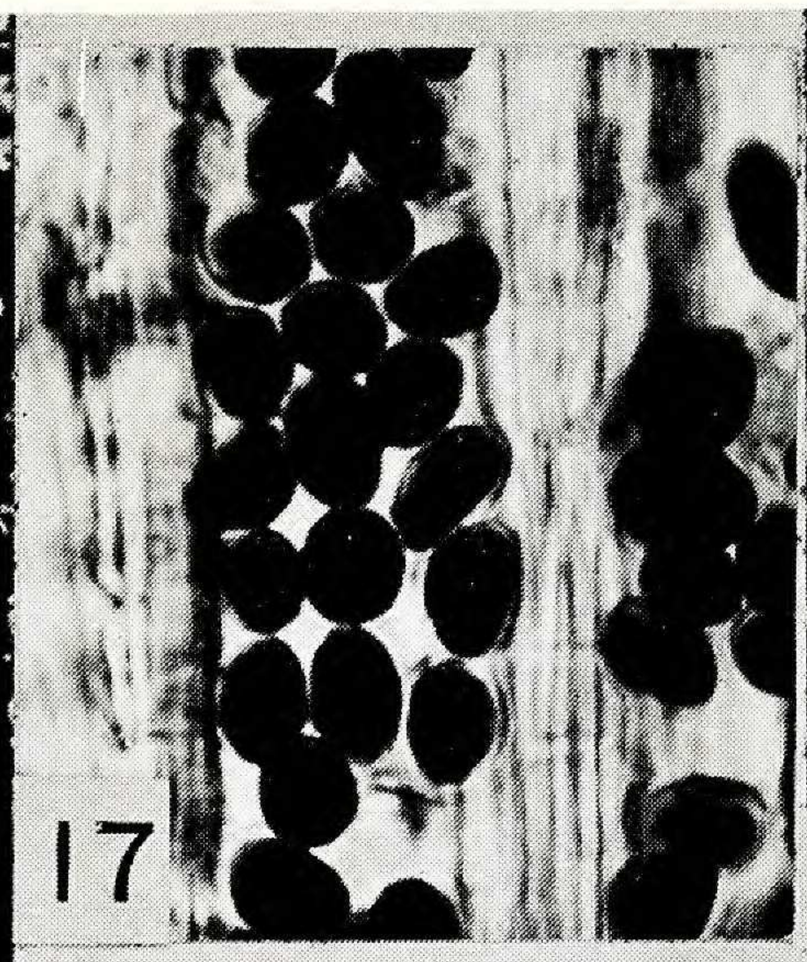
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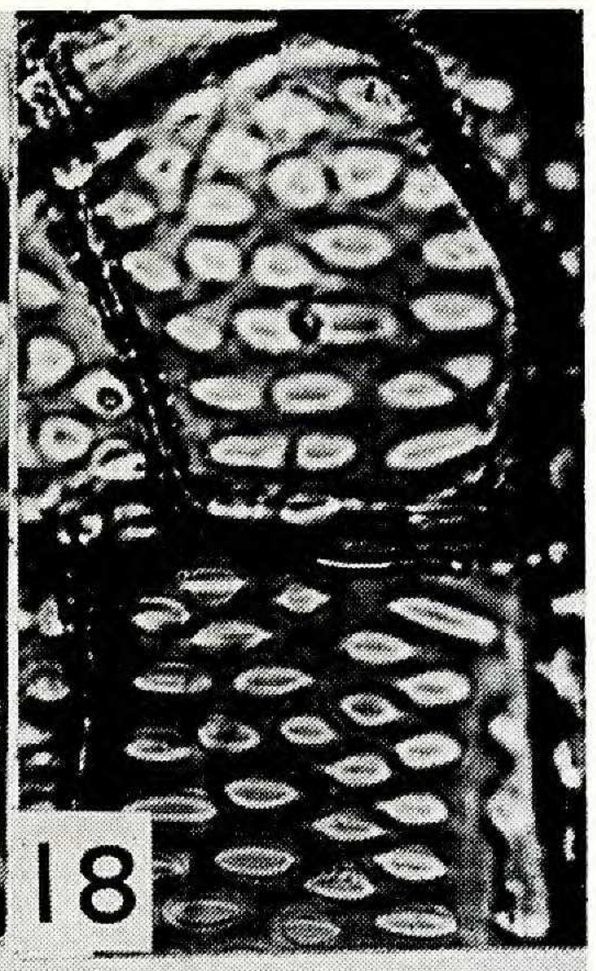
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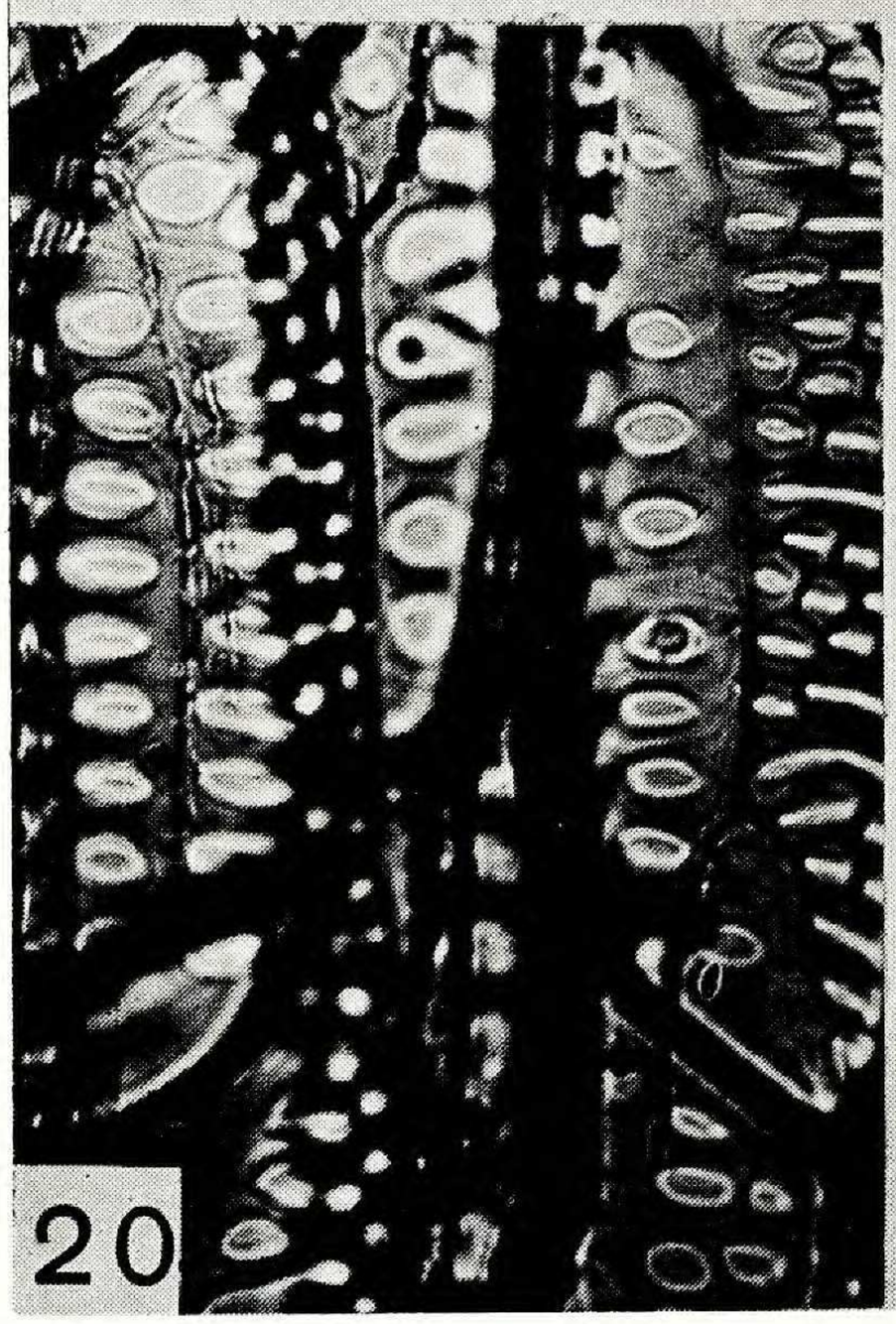
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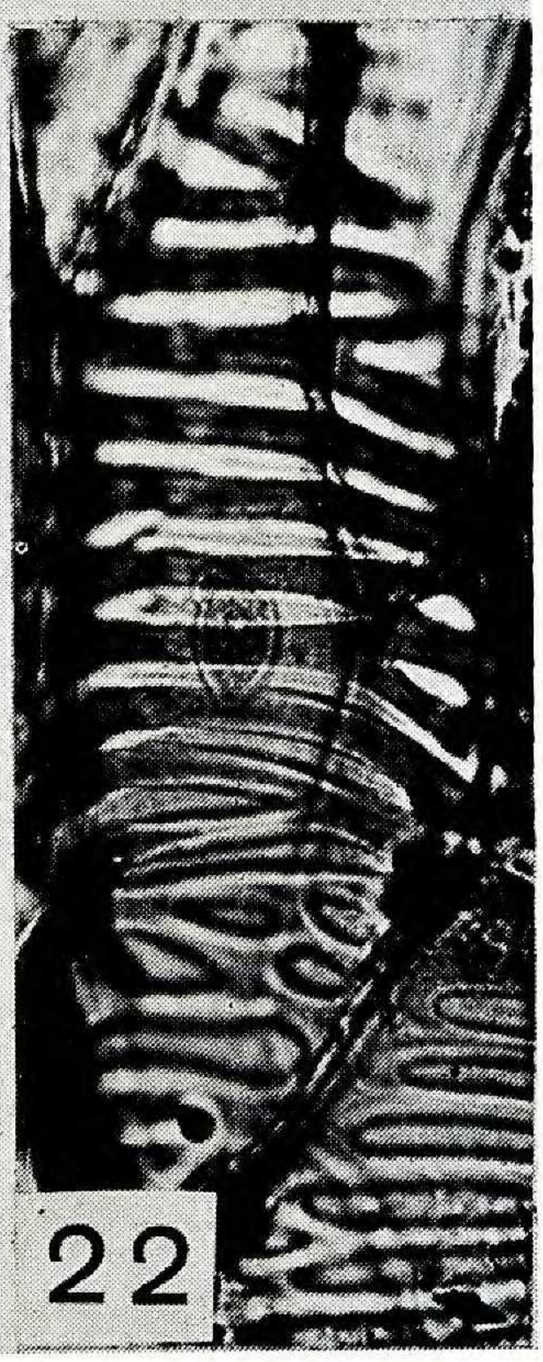
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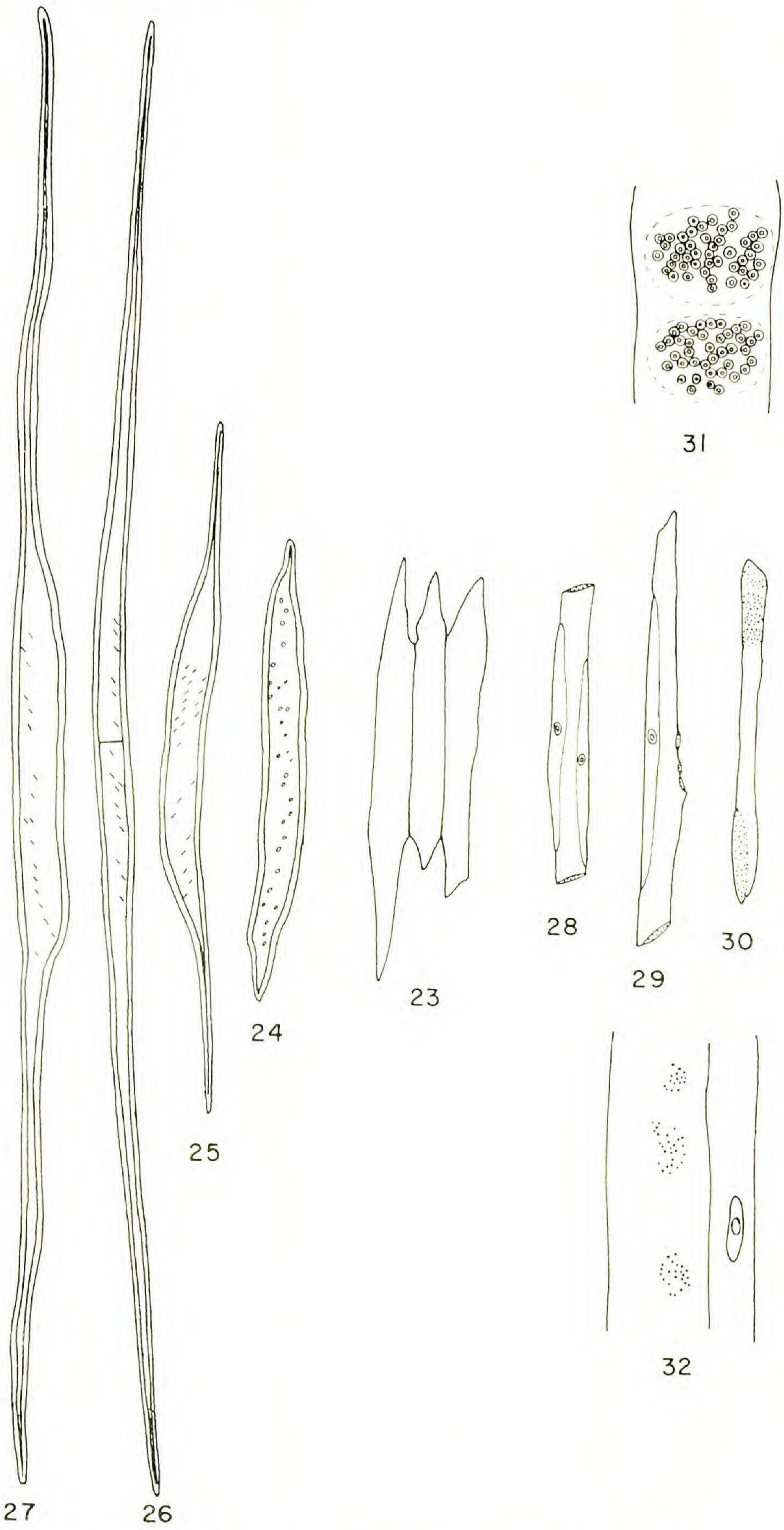

BAILEY & SRIVASTAVA, LEAF-BEARING CACTACEAE, IV